AN ANALYSIS OF SOIL MICRO-ARTHROPOD SUCCESSION

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SYNOPSIS

A disused chalk quarry in the Yorkshire Wolds contains a range of plant communities of varying successional age. These vary from late coloniser communities characterised by prostrate and rosette type plants to grassland/shrub community dominated by the grasses *Arrhenatherum elatius L.* and *Dactylis glomerata L.* and *Dactylis glomerata L.* interspersed with hawthorn *(Crataegus monogyna Jacq.)* bushes.

Analysis of both the floral and soil micro-arthropod communities in the quarry has been carried out. Following an initial plant survey in August 1975 soil samples were taken every 8 weeks. Variation in microarthropod community structure could therefore be detected on both seasonal and successsional time scales. A multivariate analysis of the data using techniques of classification and ordination has been used to show the relationships between the structure of the micro-arthropod and plant communities. The results cast light on the causal factors of succession as exhibited by both types of community.

INTRODUCTION

The study of successional processes has, and will continue to be, one of the main fields of ecological interest. As a means of studying a variety of ecological phenomena, including tolerance, competition, predation, and community structure, it provides a ready made field experiment and, as an area of research in its own right, it presents many unresolved problems. Thus the original concepts of "climax" and "facilitation" (Odum 1971) have recently been brought into question (Whittaker 1953, 1974; Slatyer 1977), and Drury & Nisbet (1971) have advocated a more integrated approach to successional studies incorporating the reciprocal effects of plant, animal, and landform components of the environment.

In view of the potential that exists in successional studies, it is perhaps surprising that animal ecologists have not entered the field in greater numbers or with greater enthusiasm than has been the case. Such studies that do examine faunal aspects of succession and community structure (e.g. Davis 1963, Hale 1966, Wood 1967, Lasebikan 1975) can usually be criticised on any of four points.

(i) The use of geographically separated sites as examples of different seral stages of a succession. Heterogeneity between sites with regard to such factors as climate, soil type, and surrounding vegetation could markedly affect the type of community present and obscure successional trends.

(ii) An ordering of these sites according to *a priori* ideas of how the succession proceeds. In cases where an objective estimate of time since the initialisation of succession can be made on the basis of historical evidence, the sites are only strictly comparable if the rate of succession is the same at each.

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(iii) Each site is assumed to be undergoing the same succession.

(iv) The measurement of community parameters based on the assumption that each site represents one homogenous community. Furthermore, it is assumed that the faunal communities are intrinsically related in structure to the surface vegetation, and that boundaries used to define plant communities can be meaningfully used to delimit animal communities. There is no reason why homogeneity of the surface vegetation should preclude heterogeneity of the associated faunal communities, or vice versa.

Ideally a successional study should be based on a single site studied over an extended period of years in such a manner that faunal and floral communities could be monitored independently, but in relation to a known successional time scale. The present study, however, attempts an objective approach to the study of successions exhibited in contemporary communities. The work describes a synecological study involving the analysis of data from both the plant and soil micro-arthropod communities of a disused chalk quarry. The quarry, situated in the Yorkshire Wolds, was abandoned between 1930 and 1955, resulting in a gradient of contemporary plant communities of varying successional age. However, the discontinuous nature of the past quarrying operations has resulted in a discrete rather than a continuous pattern of plant community structure.

The vegetation in the quarry is representative of the earlier seral stages of a chalkland succession. The climatic climax of this sere is generally ash *(Fraxinus excelsior L.)* woodland (Tansley 1939). Communities in the quarry range from almost bare ground with prostrate and rosette plants such as *Lotus corniculatus, Hieracium pilosella,* and *Leontodon hispidus,* to a grass/scrub community dominated by the grasses *Arrhenatherum elatius* and *Dactylis glomerata,* interspersed with hawthorn *(Crataegus monogyna)* bushes.

SAMPLING METHODS

The plant communities were sampled in October, 1975, by the collection of frequency data from 30 × ½m × ½m permanent quadrats. Quadrats were placed in a stratified random manner within a 21m × 10m strip of land running from the quarry face and hence perpendicularly to the observed successional sequence. Frequency data of between 0 and 25 were collected for each species on the basis of presence or absence from twenty-five 10 cm × 10 cm subsquares in each quadrat.

In October 1975, a sample of the soil micro-arthropod community associated with each quadrat was taken. Samples were taken to a maximum depth of 5 cm using a cylindrical corer of area 25.5 sq cm. A modified Tullgren funnel apparatus, operating on the basis of variable temperature and humidity and non-variable light gradients, was used to extract the micro-arthropods from each core. This sampling program was repeated on eight occasions at eight weekly intervals.

The results cited here refer to the micro-arthropods of the groups Collembola (class Insecta) and the Cryptostigmata and Mesostigmata (sub-class Acari). Data for the Collembola includes all age groups, whilse data for the Acari refers only to adult individuals. Juvenile Acari were excluded from the analysis for reasons of taxonomic difficulty and inefficiency of extraction.

RESULTS

The data matrices for the plant and animal communities were analysed using the method of principal co-ordinate analysis (Gower 1966). The method requires the extraction of the latent roots and vectors of an association matrix, in this case derived using the simple Euclidian distance measure of $d^2_{ij} = \sum_{k=1}^{v} (x_{ik} - x_{jk})^2$. Where d_{ij} is the distance between the i th and the j th quadrats and x_{ik} and x_{jk} are the numbers of the k th species in the i th and j th quadrats respectively, and v is the total number of species. The latent vectors associated with the largest latent roots correspond to the major sources of variation underlying the data and allow an ordination of the quadrats along a small number of 'principal axes'. These principal axes can often be interpreted in terms of axes of ecological variation (e.g. Blackith & Blackith 1975).

The results of a principal co-ordinate analysis on an arcsin transformation of the plant data are summarised in Fig. 1. The figure represents an ordination of the 30 quadrats along the first and second latent vectors. These vectors account for 50% and 11% of the total variance respectively. Bartlett's (1954) criteria indicate that the first latent vector is the only one of significance and hence only this vector will be discussed here.

The interpretation of this first vector is based on two assumptions.

(i) An approximate estimate of the relative 'successional age' of each quadrat is given by its distance from the quarry face. The product moment correlation coefficient of the loadings of each quadrat on the first latent vector with its distance from the quarry face is significant at $P < .001$.

(ii) In any successional sequence there are recognised 'early' and 'late' successional species. Correlating each of the 40 plant species with the first vector gives 13 coefficients significant at $P < .05$. (Table 1).

The four positive correlations are with tall grasses and 'woody' herb species, which are characteristic of a later grassland successional stage. Of the 9 negative correlations, 7 are with prostrate, rosette or pioneer type plants characteristic of a relatively early successional stage.

These observations suggest that the first latent vector can be equated with succession such that the loading of each quadrat on this vector provides an estimate of its relative

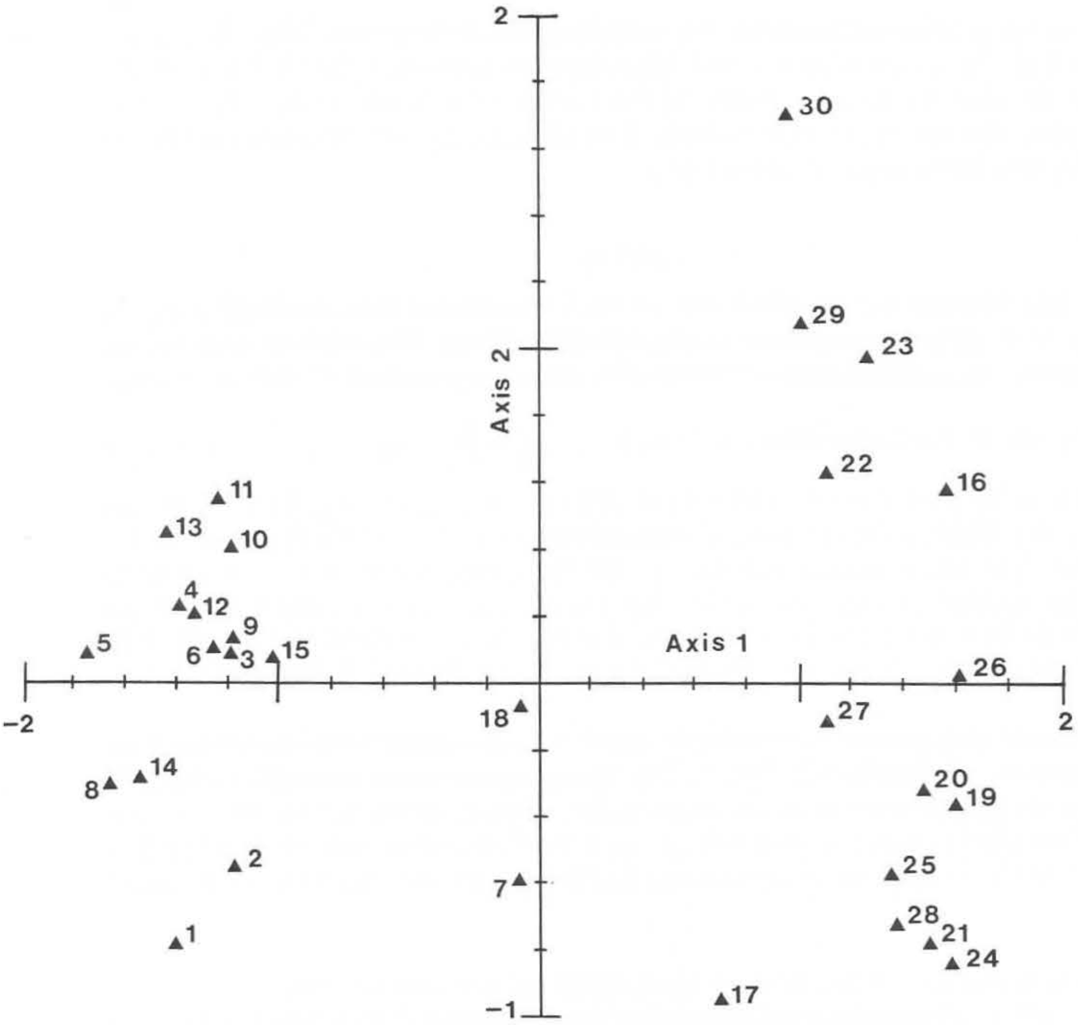

Fig. 1 Results of principal co-ordinate analysis on plant data. The 30 quadrats are shown ordinated along the first two principal axes.

successional age. On the basis of these loadings, the quadrats can be divided into two clearly separated successional groups, a division which is spatially and visually obvious in the quarry floor. The first group contains quadrat numbers 1-6 and 8-15 inclusive. This is designated the 'early' successional group and is dominated by dicotyledonous plants of a prostrate growth form. A second group, containing quadrat numbers 16, 17, and 19 to 30 inclusive, is the 'late' successional group, and represents a grassland community dominated by tall grass species and small shrubs.

Quadrats 7 and 18 fall midway between these two groups and cannot realistically be included in either. They are best regarded as examples of a transitional community.

Table 1. Correlaton of plant species with first latent vector.

Species	Relative position in succession	Correlation coefficient	Significance
Lotus corniculatus L.	early	-0.92	***
Hieracium pilosella L.	early	-0.91	***
Leontodon hispidus L.	early	-0.85	***
Gentianella amerella (L.) Borner	early	-0.65	***
Festuca ovina L.	?	-0.46	**
Medicago lupulina L.	early	-0.40	*
Euphrasia nemorosa (Pers.) Wallr.	early	-0.39	*
Plantago lanceolata L.	?	-0.36	*
Prunella vulgaris L.	early	-0.35	*
Centaurea nigra L.	late	+0.50	**
Dactylis glomerata L.	late	+0.52	**
Ononis repens L.	late	+0.92	***
Arrhenatherum elatius (L.) J. & C.Presl	late	+0.92	***

Significance given by: * $0.05 \geqslant P > 0.01$
** $0.01 \geqslant P > 0.001$
*** $0.001 \geqslant P$

Table 2 summarises the community data for the above groups. Diversity is measured using the Shannon-Weaver diversity index (Pielou 1966) given by:

$$H' = -\sum_i p_i \ln (p_i)$$

where p is the proportion of the ith species in the community. Equitability (E′) provides a measure of the evenness of species abundance within the community, and is related to diversity and the number of species (N) by:

$$E' = \exp (H')/N$$

For completeness, quadrats 7 and 18 are included in the table, but little weight can be placed on any interpretation of their results.

The "early" and "late" communities show no marked differences with respect to their community parameters, although the trend is towards a decrease in diversity as the succession reaches a grassland/ shrub community. This result is in agreement with recent literature (Williams et al. 1969, Whittaker 1975) which challenges the generally accepted view, which has been reviewed by Odum (1971), that the diversity of plant communities increases gradually during the early successional stages. It seems that, after the initial colonisation phase of succession, the growth to dominance of a few

Table 2. Community data for 'early' and 'late' successional plant communities. For explanation of parameters see text.

Quadrats	Relative successional age of group	Mean number of species/quadrat	Total number of species	H′	E′
1-6, 8-15	'early'	11.7	28	2.41	0.40
7, 18	'mid'	11.0	14	2.34	0.74
16, 17, 19-30	'late'	7.6	25	2.32	0.41

highly competitive species leads to the exclusion of many pioneer species. If these pioneer species are not replaced at a sufficient rate by new species, then there will be a drop in diversity. This drop in diversity will occur in conjunction with an increase in the total community biomass.

THE MICRO-ARTHROPOD COMMUNITIES

Over the 8 sampling periods a total of 22,217 individuals from 91 species were counted. Principal co-ordinate analyses on a log $(x + 1)$ transformation of these data for each of the 8 periods show similar patterns to that observed for the plant communities. On average the first latent vectors account for 31% (range: 24% to 35%) of the total sample variance. Furthermore, these vectors correlate significantly with each other, with distance from quarry face, and with the first plant latent vector ($P < 0.001$). Therefore in the micro-arthropod, as in the plant data, a successional trend can be recognised.

The loadings on the first latent vector give an estimate of the relative successional age of each quadrat with respect to their micro-arthropod communities. Fig. 2, illustrating the mean loadings over the eight sampling periods, shows two clearly defined groups. First, a group containing quadrats 1-15, corresponding to an 'early' successional community, and secondly a group containing quadrats 16-30, corresponding to a 'late' successional community.

The only quadrats deviating from a simple one to one relationship between plant and animal communities are numbers 7 and 18 which fell into an intermediate group with respect to their plant communities, but are clearly assigned to, respectively, 'early' and 'late' micro-arthropod communities. This result is revealing in that in each case it is the nature of the adjacent plant communities which are determining the micro-arthropod

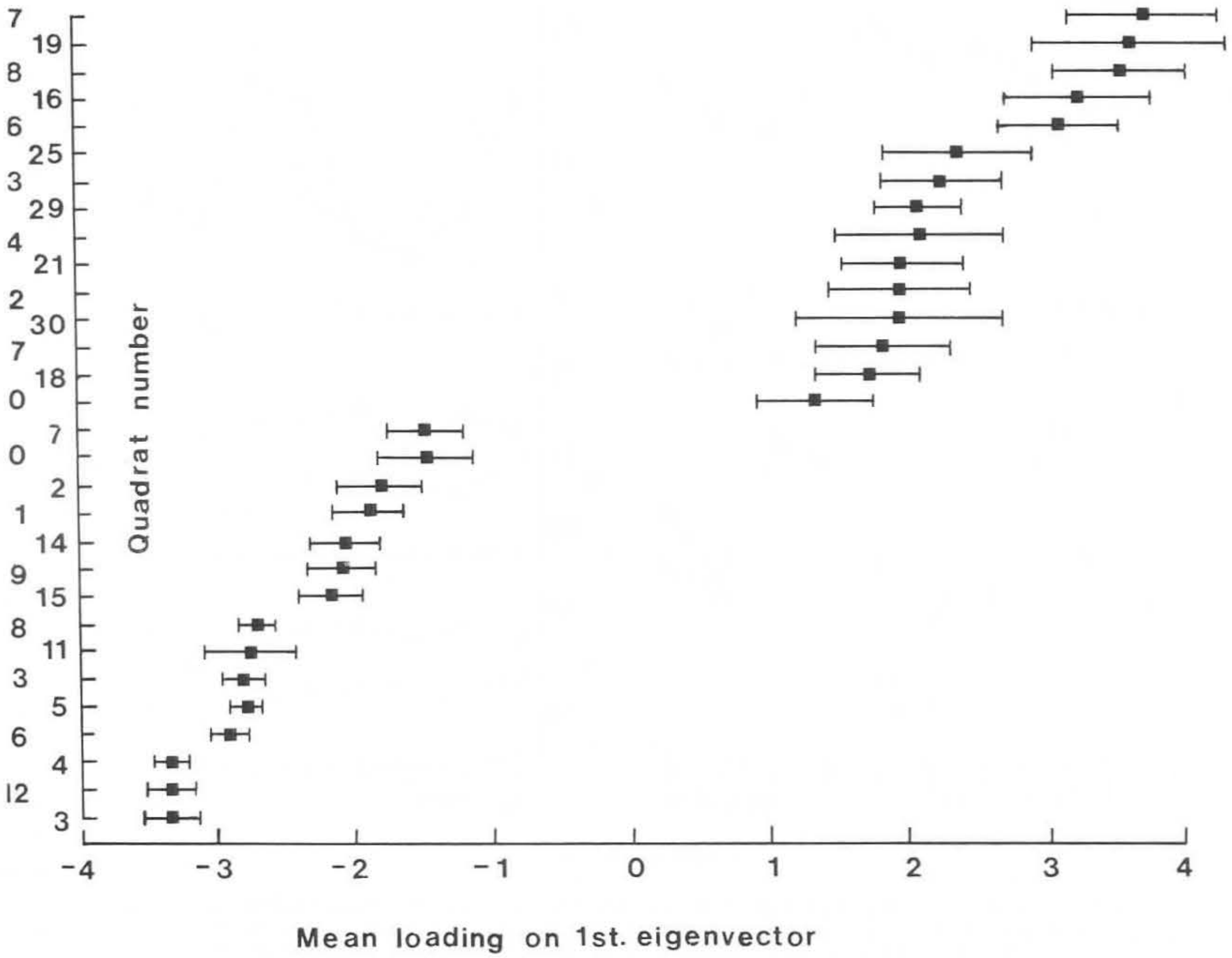

Fig. 2. Plot of mean loading in first principal axis for the 8 sets of micro-arthropod data (± standard error of mean) against a ranked order of quadrats.

community. Thus quadrat 7, which represents an island of 'older' vegetation surrounded by 'young' vegetation, has a 'young' micro-arthropod community and vice-versa for quadrat 18. This suggests that either there are subtle edaphic factors which affect the nature of the plant community, but not that of the micro-arthropod community, or that, in small 'islands' of vegetation of different successional development, the effect of immigration and competitive exclusion by surrounding populations may be the primary determinants of animal community structure.

Fig. 3 summarises the data for the 'early' and 'late' successional micro-arthropod communities. It shows that the 'late' community can be distinguished from the 'early'

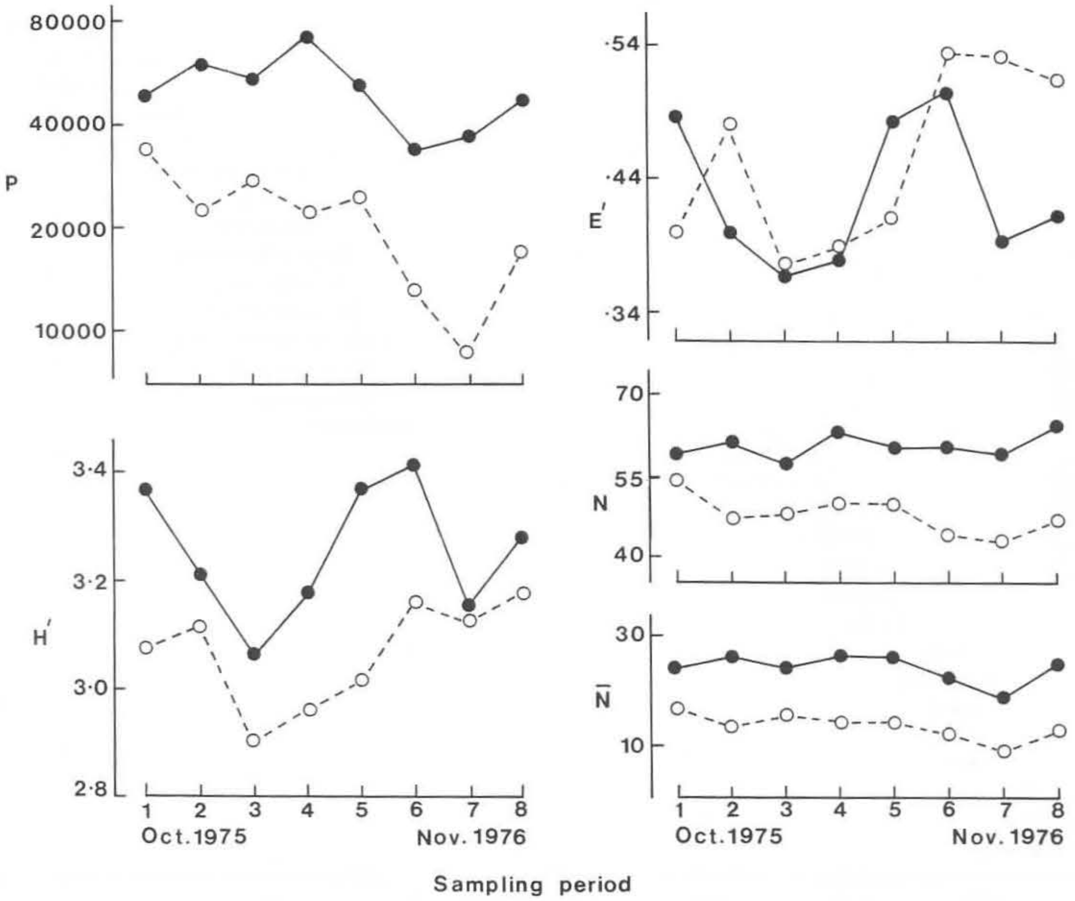

Fig. 3. Graphs showing seasonal variation in community parameters for 'early' (0—0) and 'late' (●—●) successional micro-arthropod groups. P =log density of micro-arthropods (numbers per square metre). H' = diversity. E' = equitability. N = total number of species in group. $\overline{N}$ = mean number of species per sample.

community by means of its higher population density, higher total species number, higher number of species per sample core, and higher species diversity. The difference in species diversity is a reflection of the larger number of species in the 'late' community, as equitability shows similar cyclic trends in both communities.

Three points of special interest can be made. First, despite seasonal trends in all the community parameters, the two communities remain distinct throughout the year. Secondly, the decrease in diversity shown by both communities in the third sampling period (January 1976) reflects a marked decrease in the equitably of the communities. This decrease is itself due to a decrease in the equitability of the collembola component of the community. Thirdly, the drop in population density exhibited during the summer months (sampling periods 6 and 7) is less severe in the 'late' community. The

Table 3. Micro-arthropod species showing significant successional trends ($P \leqslant .05$)

Taxa	'early' species	'late' species
Collembola	*Brachystomella parvula* (Schaffer) *Folsomides parvulus* (Stach) *Isotoma fennica* Reuter *Pseudosinella alba* (Packard) *Sminthurides assimilis* (Kraus.)	*Onychiurus armatus* (Tullb.) *Onychiurus ambulans* (Stach) *Onychiurus* sp. *Folsomia spinosa* (Ksen.) *Entomobrya nivalis* (Linn.) *Lepidocyrtus lignorum* (Favricius) *Oncopodura crassicornis* Shoebotham *Neelus minimus* Willem
Cryptostigmata	*Scutovertex minutus* (Koch) *Trichoribates incisellus* (Kram.) *Pelops tardus* (Koch)	*Belba* sp. *Damaeus* sp. *Oppia clavipectinata* (Mich.) *Xenillus tegeocranus* (Herm.) *Liebstadia similis* (Mich.) *Scheloribates confundatus* Sell. *Ceratozetes gracilis* (Mich.) *Punctoribates punctum* (Koch.) *Minunthozetes semirufus (Koch.)* *Oribatella calcarata* (Koch.) *Achipteria cleoptratus* (Linn.) *Pthiracarus piger* (Scop.) *Steganacarus striculus* (Koch.)
Mesostigmata	*Hypoaspis claviger* (Berl.)	*Pergamasus cambriensis* *Pergamasus clavipes* (Linn.) *Pergamasus* spp. (species 1 & 2) *Veigaia cervus* (Kram.) *Veigaia nemorensis* (Koch.) *Veigaia exigua* (Berl.) *Eviphis ostrinus* (Koch.) *Geholaspis mandibularis* Berl. *Geholaspis longispinosus* (Kram.) *Pachyseius humeralis* Berl. *Pachylaelaps furcifer* (Oudemans) *Rhodacarus agrestis* Karg *Hypoaspis aculeifer* (Can.) *Dinychus* sp. *Dinychura* sp.

'late' community seems to show a greater seasonal stability which can perhaps be accounted for in terms of the ameliorating effects of a denser vegetation cover. Whether or not this disparity is a yearly occurrence is, however, open to speculation, since the summer of 1976 was noted for its atypical drought conditions.

Of the total of 91 species of micro-arthropod recorded, forty six correlated significantly with the mean loading on the first eigen vector. Of these, thirty seven were positive, showing an increase in species abundance during the succession, and nine were negative (Table 3). Only one early and six 'late' successional species show no overlap between communities. Clearly the micro-arthropods show successional changes at both the specific and the community level.

DISCUSSION

The preliminary analysis of community data can be achieved by either a classification (Cormack 1971, Whittaker 1962) or an ordination (Whittaker 1967). Anderson (1965) explains that neither method is intrinsically correct, and that the choice of approach should depend on the structure of the communities sampled. The recognised pattern of species distribution along a linear environmental gradient is such that communities tend to form a continuum (Whittaker 1962). A classification procedure on such a continuum would tend to divide this single entity into a number of discrete, arbitrarily delimited communities, whereas an ordination would, by the uniform distribution of quadrats along the principal axis of variation, show the true nature of the community relationships. Only in cases where there are good *a priori* reasons for assuming a pattern of discrete communities would the classificatory approach be useful.

In the present work, the ordination of the quadrats along an axis correlated with succession allowed a direct comparison between plant and micro-arthropod communities. On the assumption that the axis represented succession, the ordination also gave information on the relative successional age of each quadrat. In classificatory procedures, such direct comparisons between groups and the relationships between members of the same group are not so clear.

The results obtained using the ordination technique of principal co-ordinate analysis have shown that a factor which can be interpreted as succession represents a major source of variation in both the plant and micro-arthropod communities of a disused chalk quarry. Furthermore, both plants and micro-arthropods show a discrete pattern of community structure, in which quadrats can be allocated to either an 'early' or 'late' successional community. The almost one to one correspondence between the two communities suggests that their patterns of community development are intrinsically related. However, it is not possible to be definitive about the associated pattern of cause and effect. Classically, the increase in micro-arthropod population density and species diversity would be attributed to an increase in the soil organic matter content, and to the general amelioration of the soil environment, both of which are associated with the increasing biomass of the surface vegetation (Davis 1963, Weis-Fogh 1948). However, the role of soil micro-arthropods in the decomposition of organic matter and the development of soils (Kubiena 1955) should not be ignored. By determining the rate and type of soil formation, micro-arthropods may considerably influence the structure and species composition of the surface vegetation.

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